HERMAN DE JONG

Institute for Systematics and Population Biology, Amsterdam

THE PHYLOGENY OF THE *TIPULA* (*LUNATIPULA*) *BULLATA* AND *FALCATA* SPECIES GROUPS (DIPTERA: TIPULIDAE)

Jong, H. de, 1995. The phylogeny of the *Tipula* (*Lunatipula*) *bullata* and *falcata* species groups (Diptera: Tipulidae). – Tijdschrift voor Entomologie 138: 245-267, figs. 1-76, tabs. 1, 2, appendices A, B. [ISSN 0040-7496]. Published 15 November 1995.
A phylogenetic analysis of the *Tipula* (*Lunatipula*) *bullata* and *falcata* species groups (Diptera: Tipulidae) is presented, based on the examination of 36 morphological characters of the adults of the currently recognized 20 species within these groups. The distribution of the species of both groups is briefly outlined. *T.* (*L.*) *cirrata* is described as new, based on material originating from south-east Spain.
H. de Jong, Department of Entomology, Institute for Systematics and Population Biology (Zoological Museum), Plantage Middenlaan 64, 1018 DH Amsterdam, The Netherlands.
Key words. – Diptera, Tipulidae, *Lunatipula*, *bullata* group, *falcata* group, phylogeny, distribution.

The phylogeny of the species of the *Tipula* (*Lunatipula*) *bullata* and *falcata* species groups is discussed as part of a research project on the historical biogeography of the western Mediterranean. Both *bullata* and *falcata* groups primarily contain western Mediterranean endemics and thus could provide clues for a better understanding of the historical biogeography of the area.

Dividing the huge genus *Tipula* Linnaeus into smaller units, Riedel (1913) was the first to distinguish a group Falcatae within the traditionally recognized Tipulae Subunicolores. The Falcatae sensu Riedel were composed of the species *bullata* Loew, *onusta* Riedel, *magnicauda* Strobl, *selenitica* Meigen, and *falcata* Riedel, five species characterized by the presence of a sickle-shaped posterior part of the inner gonostylus ['App. interm. (pars secunda) sichelförmig'; Riedel 1913: 11]. Edwards (1931) erected the subgenus *Lunatipula* within the genus *Tipula* to contain 'most of the European and North American species with unicolorous or subunicolorous wings'. Thus Riedel's Falcatae, together with other species of *Tipula*, were transferred to the subgenus *Lunatipula*.

On account of the presence of erect setae on the basal half of male sternite 8, Mannheims & Theowald (1959: 31) distinguished a *bullata* group that, besides *bullata* and *onusta*, accommodated the then newly described *bezzii*, *buchholzi*, and *subonusta*. Savchenko (1964) referred to this same unit as the *onusta* group. In his standard work on the western Palaearctic Tipulidae, Mannheims (1963-1968) proposed an array of species groups within *Lunatipula*. Mannheims

arranged the members of the Falcatae sensu Riedel into two species groups, viz. the *bullata* and *falcata* groups. The *bullata* group still contained the five species originally included in this unit (Mannheims 1967, 1968). According to Mannheims (1963, 1967), the *falcata* group is characterized by the presence of a well-developed and mostly long and posteriorly produced posterior part of the inner gonostylus, a definition which reflects Riedel's concept of the Falcatae. The *falcata* group sensu Mannheims (1967) contained 15 species of which *handschini* Mannheims, *trifasciculata* Strobl, and *zangherii* Lackschewitz, by the structure of the posterior part of the inner gonostylus, do not conform to Mannheims' definition of the group. Other character states, however, indicate a close relationship of these three species with the remaining members of the *falcata* group.

Theowald & Oosterbroek (1990) referred to Savchenko (1964) to notify the transfer of three Balkan species from the *falcata* group sensu Mannheims to the *fascingulata* species group of *Lunatipula*. Actually, Savchenko removed the Balkan inhabiting *pannonia* Loew and *jordansi* Mannheims (both as subspecies of *pannonia*) together with the Italian *zangherii* from the *falcata* group sensu Mannheims to the *fasciculata* (= *fascingulata*) group. Savchenko placed the third Balkan species of Mannheims' *falcata* group, viz. *bifasciculata* Loew, in a miscellaneous group together with most of the other species of the *falcata* group sensu Mannheims. Considering their different morphology, the removal of *bifasciculata*, *pannonia pannonia*, and *pannonia jordansi* from the *falcata*

Fig. 1. Distribution of the *Tipula* (*Lunatipula*) *bullata* species group.

group as such is fully justified. However, as the *fascingulata* group in its present-day concept is overtly non-monophyletic, their inclusion in that group does not contribute to our understanding of the systematics of *Lunatipula*. The species *zangherii* definitely belongs to the *falcata* group and is treated as such below.

More recently, the species *eyndhoveni* (Theowald 1972) and *parallela* (Theischinger 1977) were added to the *falcata* group. In Appendix A, a species of the *falcata* group originating from south-east Spain is described for the first time. Table 1 lists the species of the *bullata* and *falcata* groups as recognized here. Phylogenetic analysis of the species of the *bullata* and *falcata* groups shows that both groups most probably represent monophyletic units.

As noted above, the *bullata* and *falcata* groups have a primarily western Mediterranean distribution, and most of their species are endemic to the region. Three species, viz. *bullata*, *longidens*, and *magnicauda*, are more widely distributed and occur in central Europe as well. The distribution of the *bullata* group is given in fig. 1, that of the *falcata* group in fig. 2. More detailed maps with the ranges of the individual species of the groups will be published in a forthcoming paper on the historical biogeography of the western Mediterranean. A summary of the distribution of the species dealt with in this paper is given below. A synopsis of the distribution of all Palaearctic species of the Tipulidae can be found in Oosterbroek & Theowald (1992).

MATERIAL, METHODS AND TERMINOLOGY

Material of all species of the *bullata* and *falcata* groups, with the exception of *jativensis*, was examined (table 1). Most specimens studied are deposited in the collection of the Institute for Systematics and Population Biology (Zoological Museum), Amsterdam (ZMAN). The material consisted largely of pinned specimens, supplemented by a few alcohol preserved specimens. Additional material was borrowed from the Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn, Germany. The present depository of the holotype of *jativensis*, the only recorded specimen of this species, is unknown. Mannheims (1967) studied the at that time well-preserved specimen ('das wohlerhaltene Holotypus') from Strobl's collection and (erroneously) recorded it for both the collections at Graz and at Admont. Dr Karl Adlbauer (Graz) and Dr Elisabeth Krasser (Admont) kindly informed me that the holotype is not present in the collections under their care.

Fig. 2. Distribution of the *Tipula* (*Lunatipula*) *falcata* species group.

Preparations of the male and female terminalia were made by removing these parts and clearing them in a nearly boiling 10% KOH solution for about five minutes. After rinsing with water and 70% alcohol, the terminalia were transferred to glycerol. Examination of the specimens and their terminalia was carried out with a Wild stereo microscope, using a magnification of up to 100 ×. Drawings were made with the aid of a drawing tube attached to the microscope. Illustrations of the genital structures were made from macerated specimens. For permanent storage, the terminalia were transferred to a microvial containing some glycerol. The microvial was pinned with the relevant specimen.

The parsimony programs Hennig86, version 1.5 (Farris 1988) and PAUP, version 3.1 (Swofford 1993) were used to analyze the phylogeny. More information on the procedures followed is given in 'Discussion of adopted phylogeny'.

The terms for the structures of the Tipulidae as used in this paper are generally in accord with those employed by McAlpine (1981), with a few additions for particular features of *Lunatipula*. The term fragmentum for the structure lateral of the aedeagal guide is adopted from Rees & Ferris (1939) and Frommer (1963). Mannheims (1951 et seqq.) designated the

Table 1. The species of the *Tipula* (*Lunatipula*) *bullata* and *falcata* species groups as recognized in this paper. + : examined; – : not examined; u : unknown.

	♂	♀
***bullata* group**		
bezzii Mannheims & Theowald, 1959	+	+
buchholzi Mannheims & Theowald, 1959	+	+
bullata Loew, 1873	+	+
onusta Riedel, 1913	+	+
subonusta Mannheims & Theowald, 1959	+	+
***falcata* group**		
cirrata sp.n.	+	+
eyndhoveni Theowald, 1972	+	+
falcata Riedel, 1913	+	+
handschini Mannheims, 1967	+	u
jativensis Strobl, 1909	–	u
longidens Strobl, 1909	+	+
magnicauda Strobl, 1895	+	+
parallela Theischinger, 1977	+	+
selenaria Mannheims, 1967	+	u
selenitica Meigen, 1818	+	+
subfalcata Mannheims, 1967	+	+
subselenitica Theowald, 1957	+	+
trifasciculata Strobl, 1900	+	+
zangherii Lackschewitz, 1932	+	+
zarcoi Mannheims, 1967	+	+

same structure A9s (appendage of sternite 9). The substructures of the hypogynial valve of the female are termed according to Tjeder (1958). The terminology as adopted here is explained in figs. 4-9, 38, 58, 59, 61, 63. A recent overview of the morphology of the terminalia of Tipulidae was given by Tangelder (1985) to which paper the reader is referred for more information.

BIOLOGY

As is typical of the majority of species of the subgenus *Lunatipula*, the members of the *bullata* and *falcata* groups are adapted to relatively warm and dry environmental conditions. Species were recorded from cedar forests (*eyndhoveni*, Theowald 1972), dry oak groves (*falcata, handschini, longidens*, Dufour 1986), and dry fir woods (*magnicauda*, Dufour 1986). Mannheims (1967) supposed that *bullata* is associated with beech woods, but, although this preference to beech woods was confirmed, *bullata* can be common also in alder brakes and fir woods (Dufour 1986). Recorded altitudes usually range from about 275 m to 2000 m, with an extreme of 2800 m recorded for *selenaria* near Oukaimeden in the High Atlas of Morocco (material in ZMAN). In general, the species of the *bullata* and *falcata* groups are strong fliers and hard to catch in the field.

The species *subselenitica* is the only member of the *falcata* group of which one of the immature stages, viz. the pupa, is known. The pupa of this species, originating from humus in a cleft in the face of a limestone cliff, was described and illustrated by Theowald (1957, 1967).

SYSTEMATIC POSITION

The Palaearctic species of *Lunatipula* have been assigned to an array of species groups by Mannheims (1963, 1965a, 1966, 1967, 1968) and Savchenko (1964). In a similar way, Alexander (e.g., 1942, 1966, 1967) arranged the Nearctic species of the subgenus into smaller units. In the course of time, some of the more conspicuous species groups of *Lunatipula* were raised to subgenera of *Tipula*, viz. the *bistilata* group to *Lindnerina* (Mannheims 1965b, Mannheims & Pechlaner 1963), the *impudica* group to *Eremotipula* (Alexander 1965), the *californica* and *streptocera* groups to *Hesperotipula* (Alexander 1946, 1947), the *macrolabis* group to *Labiotipula* (Alexander 1965), and the *triplex* group to *Triplicitipula* (Alexander 1965). It is nevertheless clear that some of the above subgenera are more closely related to species groups that still remain within *Lunatipula* rather than to other subgenera of *Tipula*. (This situation can be illustrated for instance by the
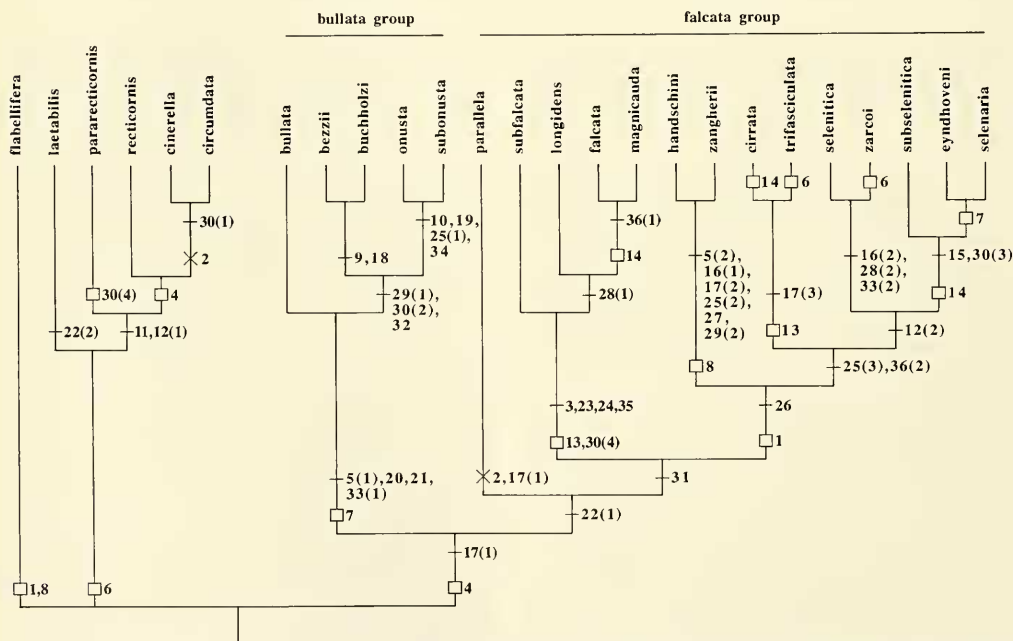

Fig. 3. Preferred tree of two equally parsimonious trees for *Tipula* (*Lunatipula*) *cinerella, circumdata, flabellifera, laetabilis, pararecticornis, recticornis*, and the species of the *T.* (*L.*) *bullata* and *falcata* species groups. Length 63, consistency index 80, retention index 92. –: synapomorphy; ☐: homoplasy; ✕: reversal.

subgenus *Labiotipula* and the *laetabilis* group of *Lunatipula* which, judging from the structure of the aedeagal guide and the intersegmental membrane of male sternites 8 and 9, are closely related). Another complicating factor in solving the higher level phylogeny of *Lunatipula* and its allies is the apparent non-monophyletic character of some of the included subgenera and species groups. A phylogenetic analysis of *Lunatipula* and its allies should start at the species level and should include not only the species of the subgenera listed above, but also those of the subgenera *Beringotipula* Savchenko, *Eumicrotipula* Alexander, *Odonatisca* Savchenko, *Pectinotipula* Alexander, *Pterelachisus* Rondani, *Ramatipula* Alexander, *Serratipula* Alexander, *Setitipula* Alexander, and *Vestiplex* Bezzi. This will indeed be a formidable task as these taxa together contain about 1200 species, i.e., more than a fourth of the total number of described species of the Tipulidae.

A first attempt to explore the phylogenetic relationships between larger groups of Palaearctic species of *Lunatipula* was published in Theowald & Oosterbroek (1990). They recognized a group Falcatae, which contained the *bullata*, *helvola*, and *falcata* groups, as the most primitive unit within *Lunatipula*. Although the majority of species currently attributed to the (non-monophyletic) *helvola* group are probably more closely related to species at present assigned to the (non-monophyletic) *fascingulata* group, I agree with Theowald & Oosterbroek that the *bullata* and *falcata* groups probably represent two of the more plesiomorphous species groups within *Lunatipula*. This conjecture can be inferred from the form of the aedeagal guide and its appendages, and from the condition of the intersegmental membrane of sternites 8 and 9 in the male. The aedeagal guide in the species of the *bullata* and *falcata* groups is a relatively simple, upright structure with at most a single posteromedial and two paired posterolateral appendages (see 'Character discussion', below). This type of aedeagal guide probably is primitive compared to the aedeagal guide of the majority of species of *Lunatipula*, which usually show additional lateral and midventral modifications. Within *Lunatipula*, a relatively simple aedeagal guide is found also in the species of the *laetabilis*, *livida*, *recticornis*, and *zimini* groups.

In the *bullata* and *falcata* groups, the intersegmental membrane between male sternites 8 and 9 is provided with two or three setal brushes of which the setae are directly implanted in the membrane (see 'Character discussion', below). The intersegmental membrane of sternites 8 and 9 carries a single medial or a pair of mediolateral setal brushes in the species of the *laetabilis*, *livida*, *recticornis*, and *zimini* groups. At present, these groups together contain about 85 species. For comparative purposes, six of these, viz. *lae-*

tabilis Zetterstedt (*laetabilis* group), *cinerella* Pierre and *circumdata* Siebke (*livida* group), *pararecticornis* Savchenko & Theischinger and *recticornis* Schummel (*recticornis* group), and *flabellifera* Savchenko (*zimini* group) were studied and included in the phylogenetic analysis of the present paper.

CHARACTER DISCUSSION

This section presents a survey of the characters used in the phylogenetic analysis of the *bullata* and *falcata* groups. The character states recognized are briefly outlined, accompanied by their respective codes, after which a more detailed discussion follows. The data are summarized in the character state matrix of table 2, where the six supplementary species of the *laetabilis*, *livida*, *recticornis*, and *zimini* groups are listed first, followed by the species of the *bullata* and *falcata* groups in alphabetical order. As the male holotype of *jativensis*, the single known specimen of this species, was not available for study, *jativensis* is not included in the following discussion. The probable phylogenetic position of *jativensis* is indicated in the 'Discussion of adopted phylogeny', below. A list of recognized autapomorphies of the species of the *bullata* and *falcata* groups is given in Appendix B.

Head

1. – Nasus: (0) present, long; (1) short or absent.

The presence of a well-developed nasus is a common feature in the Tipulidae and most probably represents a plesiomorphy within the family (fig. 10, arrow). Among the species studied, *flabellifera* and a number of species of the *falcata* group are distinguished by the presence of a very short nasus or the total absence of this structure (fig. 11). The species of the *falcata* group showing this character state are *cirrata*, *eyndhoveni*, *handschini*, *selenaria*, *selenitica*, *subselenitica*, *trifasciculata*, *zangherii*, and *zarcoi*.

Male terminalia

2. – Aedeagal guide, apical part, pair of dorsal posterolateral extensions: (0) absent; (1) present.

The aedeagal guide shows a wide variety of forms throughout *Lunatipula* and its allies. In the future, detailed study of this structure will doubtlessly lead to a better understanding of the actual higher level phylogenetic relationships within this group. Formerly, Theischinger (1977-1987) made extensive use of the shape of the aedeagal guide to classify his newly described species. Simova-Tosic & Vukovic (1983) underlined the importance of this structure for the establishment of supra-specific relationships within *Lunatipula*. Theowald & Oosterbroek (1990) presented a cladogram depicting the inferred phylogenetic relationships of six main groups of Palaearctic
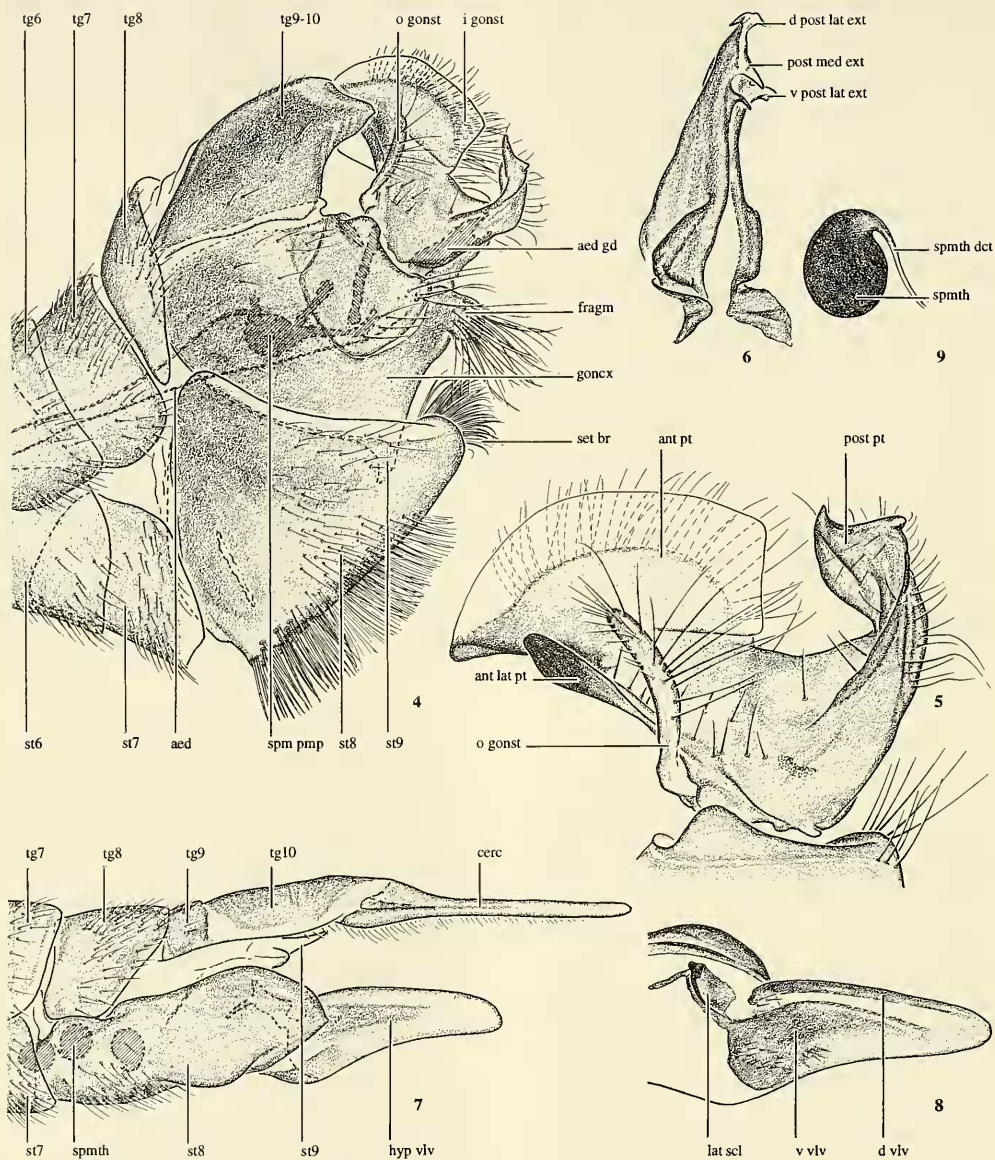
Figs. 4-9. – 4, 5, 7-9, *Tipula* (*Lunatipula*) *bullata*; 6, *T.* (*L.*) *eyndhoveni*; 4, male terminalia, lateral view; 5, left inner and outer gonostyli, lateral view; 6, aedeagal guide, posterolateral view; 7, female terminalia, lateral view; 8, right hypogynial valve, medial view; 9, spermatheca, lateral view.

Abbreviations: aed: aedeagus; aed gd: aedeagal guide; ant pt: anterior part of inner gonostylus; ant lat pt: anterolateral part of inner gonostylus; cerc: cercus; d post lat ext: dorsal posterolateral extension; d vlv: dorsal valve of hypogynial valve; fragm: fragmentum; goncx: gonocoxite; hyp vlv: hypogynial valve; i gonst: inner gonostylus; lat scl: lateral sclerotization; o gonst: outer gonostylus; post med ext: posteromedial extension; post pt: posterior part of inner gonostylus; set br: setal brush; spm pmp: sperm pump; spmth: spermatheca; spmth dct: spermathecal duct; st6 etc.: sternite 6 etc.; sut x: suture x; tg6 etc.: tergite 6 etc.; v post lat ext: ventral posterolateral extension; v vlv: ventral valve of hypogynial valve.

Lunatipula that was partly based on the structure of the aedeagal guide.

With the exception of *parallela* (fig. 19), all species of the *bullata* and *falcata* groups are distinguished by the presence of a pair of dorsal posterolateral extensions at the extreme tip of the aedeagal guide (figs. 6, 16-18, 20, 21, 74). Structures that can be interpreted as dorsal posterolateral extensions are present also in *flabellifera* (fig. 12, horizontal arrow), *pararecticornis*, and *recticornis* (fig. 14, horizontal arrow). In *laetabilis*, the apex of the aedeagal guide terminates in a pair of dorsally directed, laterally placed, and heavily scle-
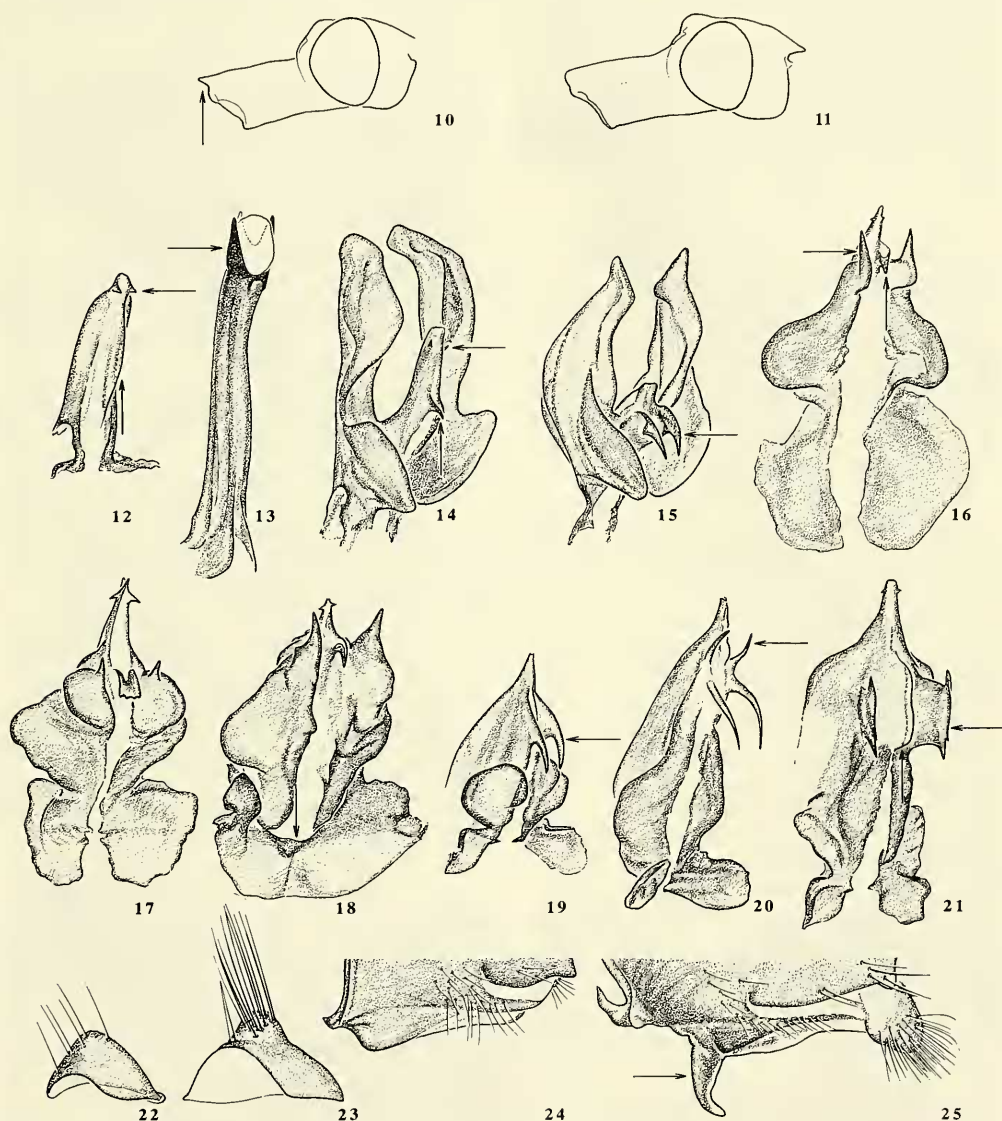
Figs. 10-25. – 10, 11, contours male head, antennae and mouthparts omitted; 10, *Tipula (Lunatipula) subfalcata*; 11, *T. (L.) handschini*; 12-21, aedeagal guide and appendages, posterolateral view; 12, *T. (L.) flabellifera*; 13, *T. (L.) laetabilis*; 14, *T. (L.) recticornis*; 15, *T. (L.) circumdata*; 16, *T. (L.) bullata*; 17, *T. (L.) bezzii*; 18, *T. (L.) onusta*; 19, *T. (L.) parallela*; 20, *T. (L.) subfalcata*; 21, *T. (L.) handschini*; 22, 23, left fragmentum, dorsal view; 22, *T. (L.) trifasciculata*; 23, *T. (L.) selenitica*; 24, 25, ventral parts of sternite 9 and gonocoxite, lateral view; 24, *T. (L.) parallela*; 25, *T. (L.) subfalcata*.

rotized triangles that enclose a medial membranous area (fig. 13, arrow). It remains to be studied whether these triangles in *laetabilis* represent the homologues of the dorsal posterolateral extensions of the species of the *bullata* and *falcata* groups.

3. – Aedeagal guide, apical part, pair of dorsal posterolateral extensions: (0) short; (1) slender and rather long, dorsally directed.

The dorsal posterolateral extensions are short in the majority of species studied (figs. 6, 12, 14, 16-18, 21, 74). The species *falcata*, *longidens*, *magnicauda*, and *subfalcata* differ from this by the presence of a pair of slender and elongate, dorsally directed posterolateral extensions at the tip of the aedeagal guide (fig. 20, arrow).

4. – Aedeagal guide, apical part, pair of ventral posterolateral extensions: (0) absent; (1) present.

With the exception of *flabellifera*, *laetabilis*, and *pararecticornis*, all species studied have a pair of ventral posterolateral extensions to the aedeagal guide (figs. 6, 14, vertical arrow, 15, arrow, 16, horizontal arrow, 17, 18, 19, arrow, 20, 21, horizontal arrow, 74). The actual shape of the extensions varies among these species (see next character).

5. – Aedeagal guide, apical part, pair of ventral posterolateral extensions: (0) ventrally curved, slender; (1) dorsally directed, slender; (2) blade-like, with serrate posterior margin.

The ventral posterior extensions of the aedeagal guide are slender and downward curved structures in the majority of species studied (figs. 6, 14, 15, 19, 20, 74). The species *bezzii*, *buchholzi*, *bullata*, *onusta*, and *subonusta* are characterized by the presence of a pair of laterally placed, dorsally directed slender extensions that are probably homologous with the ventral posterolateral extensions of the other species (figs. 16, horizontal arrow, 17, 18). The extensions terminate in an acute point in *bezzii*, *bullata*, *onusta*, and *subonusta*, in *buchholzi* their tip is rounded off.

The species *handschini* and *zangherii* are distinguished by the presence of a dorsoventrally extended and mediolaterally compressed pair of ventral posterolateral extensions (fig. 21, horizontal arrow). The posterior margins of the extensions carry a number of spinous projections, three in *handschini* and four or five in *zangherii*.

6. – Aedeagal guide, apical part, posteromedial area: (0) flat or tumid; (1) posteriorly projecting.

The posteromedial surface of the shaft of the aedeagal guide is flat to tumid in *cinerella*, *circumdata*, *laetabilis*, *pararecticornis*, *recticornis*, *trifasciculata*, and *zarcoi*. In the remainder of species studied it partly projects posteriorly. The actual condition of the projection differs among the species concerned (see next characters).

7. – Aedeagal guide, apical part, posteromedial projection: (0) a dorsoventrally extended, laterally compressed carina; (1) elongate and slender.

The species *bezzii*, *buchholzi*, *bullata*, *eyndhoveni*, *onusta*, *selenaria*, and *subonusta* are distinguished by the presence of a slender and elongate posteromedial projection (figs. 6, 16, vertical arrow, 17, 18). The posteromedial projection is present as a laterally compressed, dorsoventrally extended carina in the other species that have this part of the aedeagal guide posteriorly produced.

8. – Aedeagal guide, apical part, posteromedial carina: (0) membranous; (1) sclerotized.

The posteromedial carina of the aedeagal guide is sclerotized in *flabellifera* (fig. 12, vertical arrow), *handschini* (fig. 21, vertical arrow), and *zangherii*. In the other species with a posteromedial carina, this structure is membranous.

9. – Aedeagal guide, apical part, posteromedial slender projection: (0) about as high as broad; (1) dorsoventrally compressed.

The posteromedial slender projection of the aedeagal guide is dorsoventrally compressed in *bezzii* (fig. 17) and *buchholzi*. In the other species with a slender posteromedial projection, this structure is about as high as broad (figs. 6, 16, 18).

10. – Aedeagal guide, base: (0) ventromedially separate; (1) ventromedially fused.

The base of the aedeagal guide consists of a pair of – usually well-separated – posteroventral extensions in the majority of species studied (figs. 6, 12-17, 19-21, 74). As a special feature, the base of the aedeagal guide forms a broad sclerotized bridge in *onusta* and *subonusta* (fig. 18, arrow).

11. – Aedeagal guide, large two-lobed and compressed gonapophysis: (0) absent; (1) present.

Among the species studied, *cinerella*, *circumdata* (fig. 15), *pararecticornis*, and *recticornis* (fig. 14) are characterized by the presence of a pair of large two-lobed and mediolaterally compressed gonapophyses that flank the aedeagal guide. Similar structures are present in all species of the *Lunatipula livida* and *recticornis* species groups, and in the species of the subgenera *Eumicrotipula* and *Pectinotipula*.

12. – Fragmentum: (0) variously shaped; (1) ventrally produced into slender extension; (2) coneshaped, constricted near midheight.

The fragmentum shows a wide range of shapes
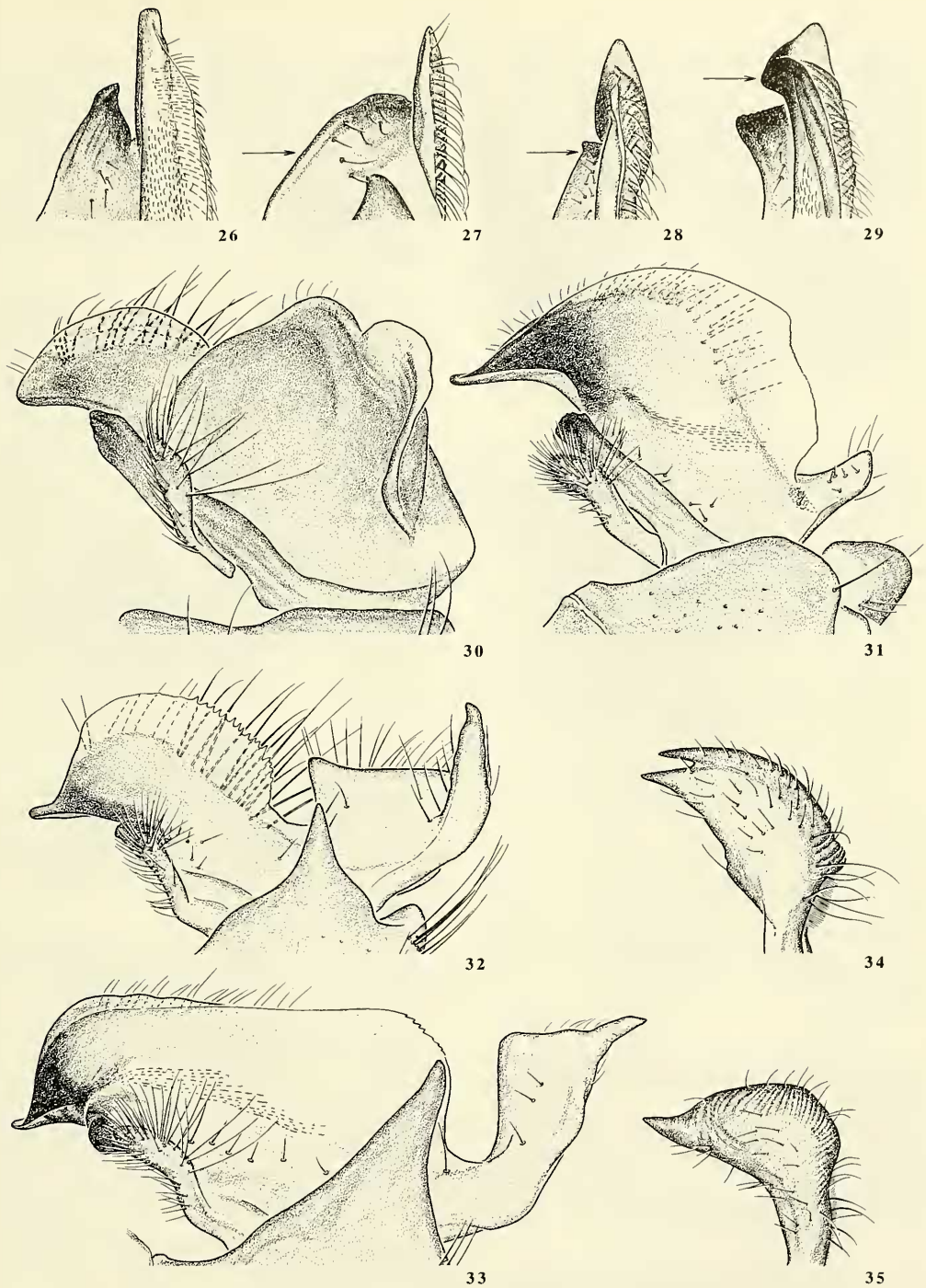
Figs. 26-35. – 26-29, anterior apices of anterior and anterolateral parts of left inner gonostylus, dorsal view; 26, *Tipula (Lunatipula) bullata*; 27, *T. (L.) handschini*; 28, *T. (L.) selenitica*; 29, *T. (L.) subselenitica*; 30-33, left inner gonostylus lateral view; 30, *T. (L.) handschini*; 31, *T. (L.) trifasciculata*; 32, *T. (L.) selenitica*; 33, *T. (L.) subselenitica*; 34, 35, apex of posterior part, posterior view; 34, *T. (L.) bullata*; 35, *T. (L.) bezzii*.

throughout *Lunatipula*. It can be low or elongate, ventrally, posteriorly or dorsally directed, with its apex pointing posteriorly or medially. Its tip can be adorned with a pencil of long or short setae, or it can be covered with spinous points. Among the species studied, a slender and ventrally produced fragmentum was studied in *cinerella, circumdata, pararecticornis*, and *recticornis*. The majority of species of the *bullata* and *falcata* groups are distinguished by a relatively low or evenly conically shaped broad-based fragmentum (figs. 22, 71). The species *eyndhoveni, selenaria, selenitica, subselenitica*, and *zarcoi* differ from this by the presence of a cone-shaped fragmentum that is distinctly narrowed in its apical half (fig. 23).

13. – Gonocoxite, midventral area: (0) tumescent; (1) with long conical projection.

The midventral area in between the gonocoxites is membranous and evenly curved without further modifications in the majority of species studied (fig. 24). The species *cirrata, falcata, longidens, magnicauda, subfalcata, trifasciculata*, and the unexamined *jativensis* are distinguished by the presence of a long and conical extension in the anterior part of the midventral membrane. The projection is anteriorly and laterally sclerotized in *falcata, longidens, magnicauda*, and *subfalcata* (fig. 25, arrow), in *cirrata* and *trifasciculata* (and probably also in *jativensis*) it is entirely membranous (fig. 69).

14. – Inner gonostylus, anterior part: (0) short, at most about 1.5 times as long as high; (1) elongate, about 2 times as long as high.

The anterior part of the inner gonostylus of the majority of species studied is a rather short structure that can be up to about 1.5 times as long as high (figs. 5, 30-32). The species *cirrata, eyndhoveni, falcata, magnicauda, selenaria*, and *subselenitica* have a long anterior part that is about 2 times as long as high (figs. 33, 70).

15. – Inner gonostylus, anterior part, apex (dorsal view): (0) relatively long and gradually narrowing towards tip; (1) short and broad.

The anterior part of the inner gonostylus in the majority of species studied is mediolaterally compressed and slender when seen in dorsal view (fig. 26-28), whereas it is short and plump in *eyndhoveni, selenaria*, and *subselenitica* (fig. 29, arrow).

16. – Inner gonostylus, anterolateral part (dorsal view): (0) relatively narrow, lateral margin moderately convex to concave; (1) broad, lateral margin strongly diverging from anterior part; (2) lateral margin with sharp emargination.

When seen in dorsal view, the anterolateral part of the inner gonostylus appears as a relatively narrow structure with a moderately convex to concave lateral margin in most species studied (figs. 26, 29). The species *handschini* and *zangherii* are distinguished by the presence of a broad anterolateral part of which the lateral margin diverges strongly from the anterior part (fig. 27, arrow). In *selenitica* and *zarcoi* there is a rather sharp emargination near the anterior apex of the anterolateral part (fig. 28, arrow).

17. – Inner gonostylus, posterior part: (0) a well-developed blade; (1) an elongate structure with laterally produced tip; (2) huge, shell-like; (3) small.

The posterior part of the inner gonostylus is a well-developed blade-like structure in the majority of species of *Lunatipula*. Among the species studied, this situation is present in *cinerella, circumdata, flabellifera, laetabilis, parallela, pararecticornis*, and *recticornis*. The posterior part is present as an elongate structure with a laterally produced, and in most cases slender, tip in *bezzii, buchholzi, bullata* (fig. 5), *eyndhoveni, falcata, longidens, magnicauda, onusta, selenaria, selenitica* (fig. 32), *subfalcata, subonusta, subselenitica* (fig. 33), and *zarcoi*. In *handschini* and *zangherii* the posterior part consists of a large and laterally concave shell-like structure (fig. 30). A very small posterior part is present in *cirrata* (fig. 70) and *trifasciculata* (fig. 31).

18. – Inner gonostylus, posterior part, surface: (0) even; (1) with closely placed parallel grooves.

The surface of the posterior part of the inner gonostylus is even in most species studied (fig. 34). Both *bezzii* and *buchholzi* are distinguished by the textured posterodorsal surface of the conically elongate posterior part which shows a large number of closely placed parallel grooves (fig. 35).

19. – Outer gonostylus: (0) widening in apical part, usually short and broad; (1) narrowing in apical part, remarkably slender.

The shape of the outer gonostylus varies considerably within *Lunatipula*, but the structure is usually rather short and broadens in its apical part (fig. 36). Most species studied conform to this state, with the exception of *laetabilis, onusta*, and *subonusta*. In *laetabilis* the outer gonostylus is relatively slender, but widens in the apical portion. In *onusta* and *subonusta* it is elongate and very slender, and narrows towards its tip (fig. 37).

20. – Sperm pump, posterior apodemes: (0) separate up to lumen of sperm pump; (1) basally connected by sclerotized plate.

The species of the *bullata* group, viz. *bezzii, buchholzi, bullata, onusta*, and *subonusta*, differ from the other species studied by the presence of a sclerotized connection between the bases of the posterior apo-
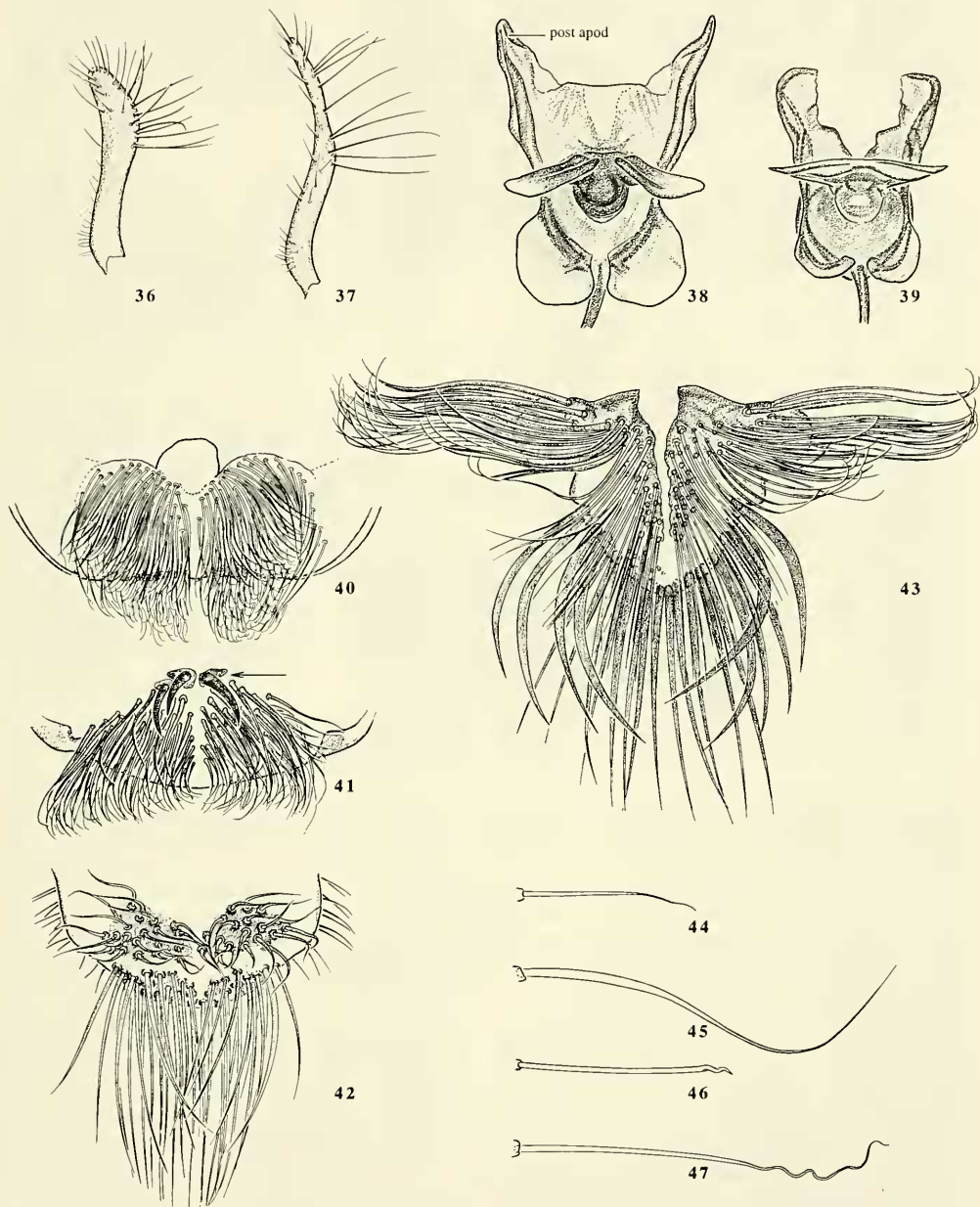
Figs. 36-47. – 36, 37, left outer gonostylus, lateral view; 36, *Tipula* (*Lunatipula*) *bezzii*; 37, *T.* (*L.*) *onusta*; 38, 39, sperm pump, dorsal view; 38, *T.* (*L.*) *bullata*; 39, *T.* (*L.*) *parallela*; 40-43, setal brushes on intersegmental membrane sternite 8 and 9, posterior view; 40, *T.* (*L.*) *bezzii*; 41, *T.* (*L.*) *onusta*; 42, *T.* (*L.*) *parallela*; 43, *T.* (*L.*) *subfalcata*; 44-47, representative seta from dorsolateral setal brush; 44, *T.* (*L.*) *parallela*; 45, *T.* (*L.*) *subfalcata*; 46, *T.* (*L.*) *handschini*; 47, *T.* (*L.*) *cirrata*. Abbreviation: post apod: posterior apodeme.
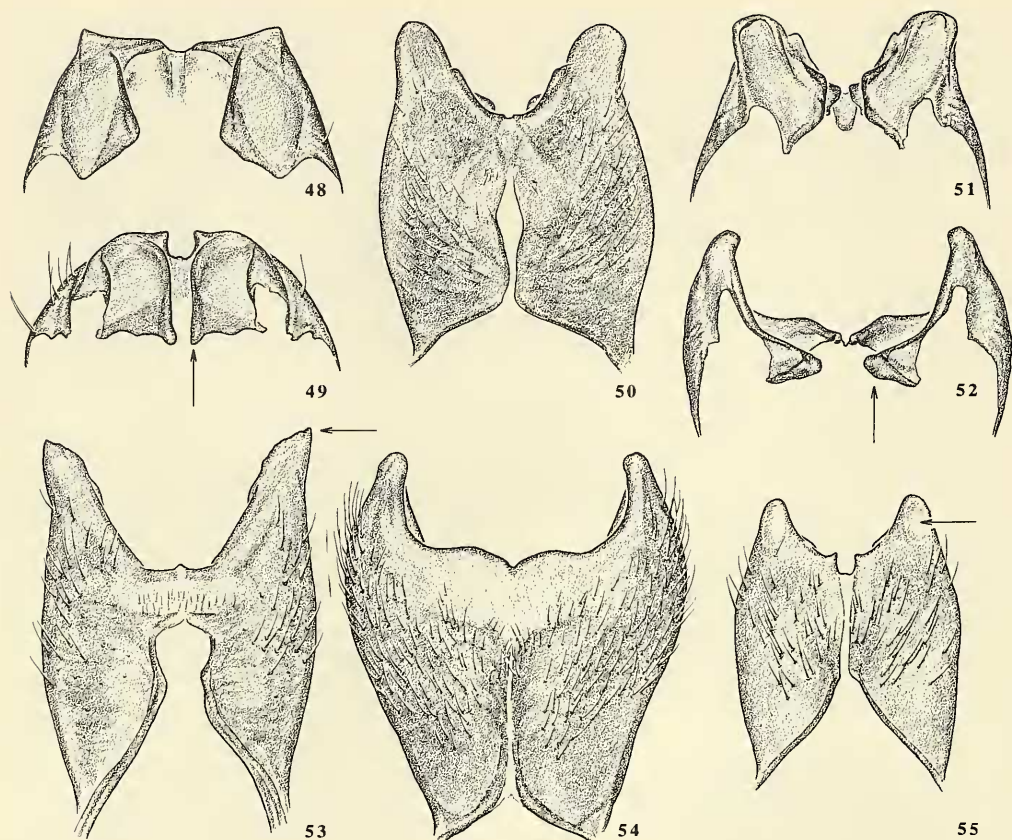
Figs. 48-55. – 48, 49, 51, 52, posterior portion of male tergite 9-10, ventral view; 50, 53-55, male tergite 9-10, dorsal view; 48, *Tipula* (*Lunatipula*) *bullata*; 49, *T.* (*L.*) *bezzii*; 50, 51, *T.* (*L.*) *subfalcata*; 53, *T.* (*L.*) *longidens*; 52, 54, *T.* (*L.*) *handschini*; 55, *T.* (*L.*) *selenitica*.

demes (fig. 38). The posterior apodemes are separate structures up to the body of the sperm pump in the other species examined (fig. 39).

21. – Sternite 8: (0) covered with scattered decumbent setae; (1) anterior part with concentration of erect long setae.

Sternite 8 in the Tipulidae is usually covered with scattered decumbent setae, a character state found also in the majority of species of *Lunatipula* and doubtlessly representing a plesiomorphy (fig. 69). The species *bezzii*, *buchholzi*, *bullata*, *onusta*, and *subonusta* differ from the remainder of species examined by the presence of a concentration of long and erect setae on the anterior half or more of sternite 8 (fig. 4). The erect setae are confined to the ventro-medial part of the sternite. Most setae are slender, but in *bullata* (fig. 4), and to a much lesser extent in

bezzii and *subonusta*, the setae implanted near the anterior margin of the sternite are stronger than the others.

22. – Sternites 8 & 9, intersegmental membrane, setal brushes: (0) one (paired) brush; (1) three brushes; (2) four brushes.

The intersegmental membrane in between sternites 8 and 9 is generally adorned with one or more setal brushes in the species of *Lunatipula*. Among the species studied, a single medial brush or one pair of medial brushes is present in *cinerella*, *circumdata*, *flabellifera*, *pararecticornis*, *recticornis*, *bezzii*, *buchholzi*, *bullata*, *onusta*, and *subonusta* (figs. 40, 41). The species *laetabilis* is characterized by the presence of four setal brushes arranged in two pairs. All other species studied are distinguished by the presence of three setal brushes on the intersegmental membrane,

consisting of a pair of dorsal brushes and a single ventromedial one (figs. 42, 43, 73; see next two characters).

23. – Sternites 8 & 9, intersegmental membrane, setal brushes, area of insertion: (0) oval shaped, laterally extended; (1) dorsal brushes ventrally extended, elongate.

The area of insertion of the setal brushes on the intersegmental membrane of sternites 8 & 9 is wider than long and more or less oval in shape in the majority of species studied (figs. 40-42, 73). In *falcata, longidens, magnicauda*, and *subfalcata* the dorsal brushes are ventrally extended. The ventrally orientated extensions provide the brushes a V-shaped appearance when seen in posterior view (fig. 43).

24. – Sternites 8 & 9, intersegmental membrane, setal brushes, area of insertion: (0) oval shaped, laterally extended; (1) ventromedial brush strongly protruding, margin semi-circular.

As noted above, the area of insertion of the setal brushes on the intersegmental membrane of sternites 8 & 9 is oval shaped in most of the examined species. A different condition occurs in *falcata, longidens, magnicauda*, and *subfalcata*. In these species, the setae of the ventromedial brush are arranged in a semi-circular formation and the brush protrudes as a tongue-like extension (fig. 43).

25. – Sternites 8 & 9, intersegmental membrane, setal brushes, condition of setae: (0) slightly curved and slender; (1) thorn-like (in part); (2) short and stout (in part); (3) strong (in part).

The setae of the setal brushes on the intersegmental membrane of sternites 8 & 9 are generally slightly curved and slender in the majority of species studied (figs. 44, 45). The species *onusta* and *subonusta* differ from the other examined species by the presence of one or two pairs of thorn-like setae in the dorsal part of the setal brushes (fig. 41, arrow). The setae of the dorsal setal brushes are remarkably short and stout in *handschini* and *zangherii* (fig. 46). The species *cirrata, eyndhoveni, selenaria, selenitica, subselenitica, trifasciculata*, and *zarcoi* are distinguished by the presence of two to four strong lateral setae that are about two times as thick as the remainder of setae in the ventromedial brush (fig. 73).

26. – Sternites 8 & 9, intersegmental membrane, setal brushes, condition of setae: (0) slightly curved; (1) frizzled at tip (in part).

The setae of the setal brushes on the intersegmental membrane between sternites 8 and 9 are usually slightly curved in the majority of species examined (figs. 44, 45). However, the setae of the dorsal brushes are frizzled at their tips in *cirrata, eyndhoveni, handschini, selenaria, selenitica, subselenitica, trifasciculata, zangherii*, and *zarcoi* (figs. 46, 47). The extent to which the apices of the setae are curled is less in both *handschini* and *zangherii* compared with the other species involved. According to the illustrations given by Mannheims (1967), the unexamined *jativensis* also has frizzled setae in the dorsal brushes.

27. – Tergite 9-10: (0) lateral margins evenly curved, tergite of equal width throughout (dorsal view); (1) tergite widening towards posterior margin.

Seen in dorsal view, tergite 9-10 appears to be more or less parallel-sided in the majority of species examined. The lateral margins are slightly curved, with the widest portion of the tergite lying at about midlength (figs. 50, 53, 55, 72). The species *handschini* and *zangherii* deviate from this norm by having tergite 9-10 distinctly widening towards the posterior margin (fig. 54).

28. – Tergite 9-10, posterolateral extensions: (0) tip rounded (dorsal view), dorsal surface convex; (1) elongate, tip laterally angular; (2) dorsal surface concave.

Among the species studied, the posterolateral extensions of tergite 9-10 vary considerably in shape, but mostly they are relatively short and more or less rounded (figs. 48-52, 54, 55). The species *falcata, longidens*, and *magnicauda* differ from the remainder of examined species by the long and laterally acutely pointed posterolateral extensions of tergite 9-10 (dorsal view, fig. 53, arrow).

The dorsal surface of the posterolateral extensions of tergite 9-10 is convex in the majority of examined species. Two species of the *falcata* group, viz. *selenitica* and *zarcoi*, are distinguished by a concave dorsal surface of the extensions. The concave area covers the extreme tip of the extensions in *selenitica* (fig. 55, arrow), in *zarcoi* it extends further anteriorly.

29. – Tergite 9-10, ventral sclerotizations: (0) medially wide apart, relatively long; (1) medially approximate, anteromedial corner produced; (2) short, medially projecting.

In most species examined, the ventral sclerotizations near the posterior margin of tergite 9-10 consist of a pair of widely separate and well-developed plates of which the medial margins run more or less parallel for some distance (figs. 48, 51). The species *bezzii, buchholzi, onusta*, and *subonusta* are distinguished by the close approximation of the ventral sclerotizations. The anteromedial corners of the ventral sclerotizations are anteriorly produced in these four species (fig. 49, arrow). The species *handschini* and *zangherii* differ from the other species studied by the short and medially directed ventral sclerotizations (fig. 52, arrow).
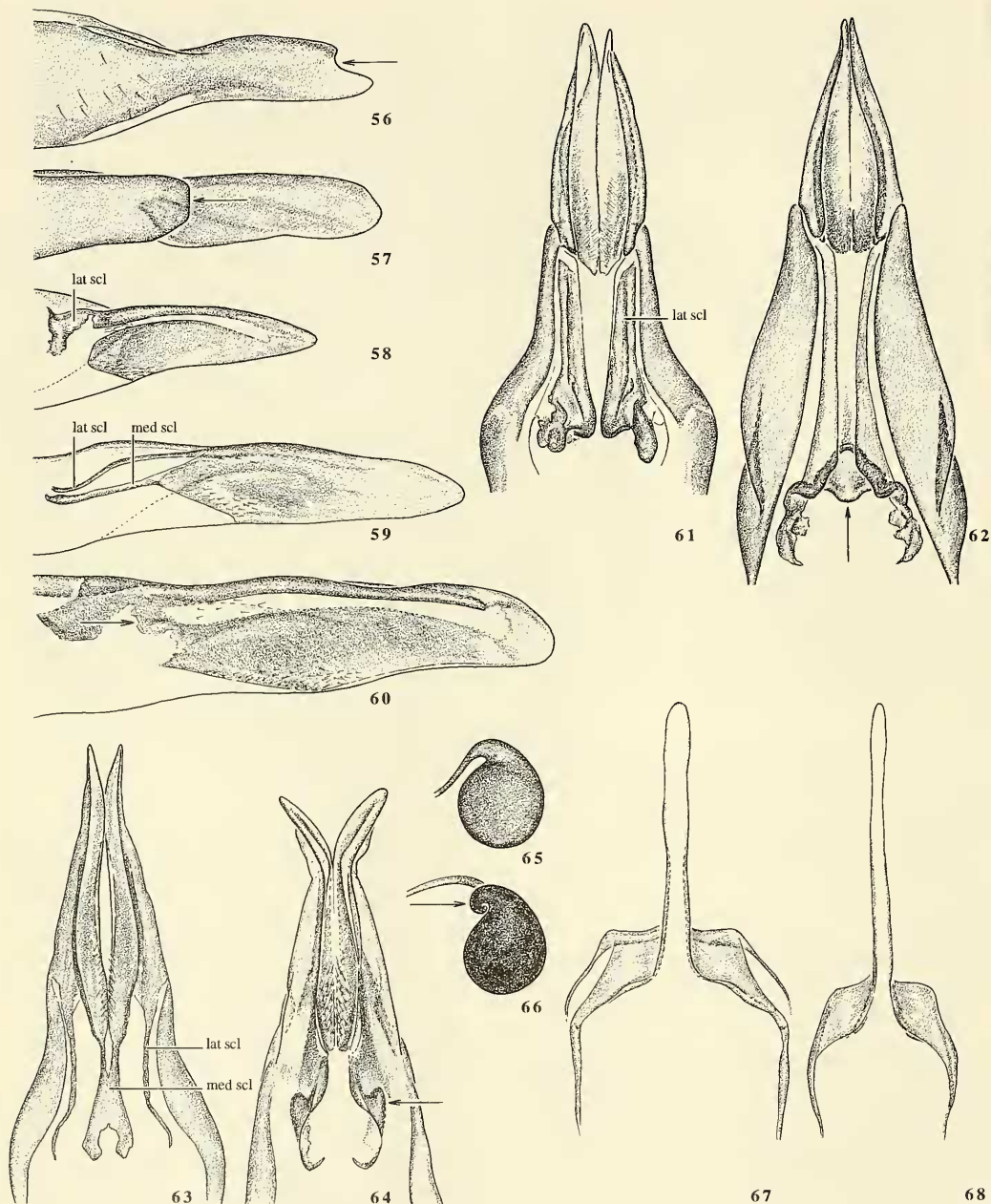
Figs. 56-68. – 56, 57, sternite 8 and left hypogynial valve, lateral view; 56, *Tipula* (*Lunatipula*) *circumdata*; 57, *T.* (*L.*) *bezzii*; 58-60, right hypogynial valve, medial view; 58, *T.* (*L.*) *parallela*; 59, *T.* (*L.*) *subfalcata*; 60, *T.* (*L.*) *subselenitica*; 61-64, sternite 8 and hypogynial valves, dorsal view; 61, *T.* (*L.*) *bezzii*; 62, *T.* (*L.*) *onusta*; 63, *T.* (*L.*) *subfalcata*; 64, *T.* (*L.*) *selenitica*; 65, 66, spermatheca and base spermathecal duct; 65, *T.* (*L.*) *parallela*; 66, *T.* (*L.*) *subfalcata*; 67, 68, female sternite 9, ventral view; 67, *T.* (*L.*) *longidens*; 68, *T.* (*L.*) *falcata*.
Abbreviations: lat scl: lateral sclerotization; med scl: medial sclerotization.

Female terminalia

30. – Hypogynial valves: (0) well-developed, tapering towards rounded tip (lateral view), dorsal and ventral valves separate; (1) tip emarginate; (2) short, almost parallel sided; (3) dorsal and ventral valves anteriorly connected; (4) dorsal and ventral valves entirely fused.

Most species of *Lunatipula* have well-developed hypogynial valves in the female, a situation doubtlessly representing the plesiomorphous condition within the subgenus. The hypogynial valves in this state are usually tapering towards a more or less rounded tip (figs. 57-60, 75). Among the species studied, both *cinerella* and *circumdata* are distinguished by the emarginate tip of the hypogynial valves, a condition that probably represents a synapomorphy for the species of the *livida* group (fig. 56, arrow). The species *bezzii*, *buchholzi*, *onusta*, and *subonusta* differ from the other species studied by their short and almost parallel-sided hypogynial valves (fig. 57). The species *eyndhoveni* and *subselenitica* are unique among the examined species in having a sclerotized connection at the base of the dorsal and ventral valves (fig. 60, arrow). The female of *selenaria* remains unknown, but may also show the latter condition. Complete fusion of the dorsal and ventral valves is found in *falcata*, *longidens*, *magnicauda*, and *subfalcata* (fig. 59).

31. – Spermatheca, base of spermathecal duct: (0) evenly curved; (1) making a loop.

The spermathecal duct gradually curves away from the spermatheca in the greater majority of the Tipulidae, a condition found also in the majority of species examined (fig. 65). A different condition is found in *cirrata*, *eyndhoveni*, *falcata*, *longidens*, *magnicauda*, *selenitica*, *subfalcata*, *subselenitica*, *trifasciculata*, *zangherii*, and *zarcoi*, where the base of the spermathecal duct shows a clockwise or counterclockwise rotation (fig. 66, arrow). The direction of the rotation of the spermathecal duct can vary intraspecifically. The females of *handschini*, *jativensis*, and *selenaria* remain unknown, but may also show a twisted base of the spermathecal duct.

32. – Sternite 8, lateroposterior apex: (0) tapering and usually gradually merging with hypogynial valve; (1) broad, truncate.

Lateroposreriorly, sternite 8 tapers and gradually merges with the hypogynial valve or terminates in an acute point that is separate from the hypogynial valve in the majority of species examined (figs. 7, 56, 75). In *bezzii*, *buchholzi*, *onusta*, and *subonusta* the lateroposterior end of sternite 8 is broad and truncate (fig. 57, arrow).

33. – Sternite 8, lateral sclerotization: (0) fused with dorsal valve of hypogynial valve, unmodified; (1) separate from dorsal valve; (2) with cavity.

Within *Lunatipula*, the dorsal valves of the hypogynial valves are often extended into a sclerotization that lies lateral within sternite 8. In most species examined, the dorsal valves are connected with these lateral sclerotizations (fig. 58). The species *bezzii*, *buchholzi*, *bullata*, *onusta*, and *subonusta* are distinguished by the presence of a membranous gap in between the base of the dorsal valve and the accompanying anterior sclerotization. In *bullata* the sclerotization is short and fused with the anterodorsal part of the ventral valve (fig. 8), in the four other species the sclerotization is elongate and lies entirely free from the hypogynial valves (figs. 61, 62). The lateral sclerotization is relatively flat in most of the examined species, but *selenitica* and *zarcoi* show a posteriorly directed cavity in this structure (fig. 64, arrow).

34. – Sternite 8, lateral sclerotizations: (0) separate; (1) anteriorly fused.

The lateral sclerotizations at the base of the hypogynial valves are separate in most of the examined species (figs. 61, 63, 64). Both *onusta* and *subonusta* differ from the remainder of species studied by the presence of a sclerotized bridge that connects the anterior tips of the lateral sclerotizations (fig. 62, arrow).

35. – Sternite 8, medial sclerotization: (0) absent; (1) present.

In the majority of females examined, sternite 8 contains at most a pair of lateral sclerotizations (figs. 61, 62, 64). A unique feature is found in *falcata*, *longidens*, *magnicauda*, and *subfalcata*, where an elongate medial sclerotization stretches anteriorly from its attachment to the anterior margin of the ventral valves (figs. 59, 63).

36. – Sternite 9, posterior extension: (0) relatively short, at most 1.5 times width of sternite 9, about as high as broad; (1) about two times as long as width of sternite 9; (2) dorsoventrally compressed, broad.

The females of *falcata* and *magnicauda* are distinguished among the species examined by the elongate posterior extension of sternite 9. In these two species the posterior extension is about two times as long as the width of sternite 9 (fig. 68), whereas it usually is much shorter in the other species (figs. 67, 76). A few species of the *falcata* group are distinguished by the presence of a disk-like dorsoventrally compressed and broad posterior extension of sternite 9. The species concerned are *cirrata*, *eyndhoveni*, *selenitica*, *subselenitica*, *trifasciculata*, and *zarcoi*. The extension is extremely broad and terminates in an emarginate apex in *cirrata* (fig. 76). In the other species with a broad and flat posterior extension, the structure is less broad and terminates in an acute tip. Note that the female of *selenaria* is unknown, but probably also shows the

latter character state.

DISCUSSION OF ADOPTED PHYLOGENY

The character state matrix given in table 2 was analyzed with the parsimony programs Hennig86 and PAUP. In table 2, unknown characters are coded '?' and inapplicable characters '-' for matters of reference only. Platnick et al. (1991) discussed the potentially different treatment of such missing entries by Hennig86 and PAUP. Maddison (1993) discussed the consequences of coding inapplicable characters as missing data. In the analysis presented here, multistate characters were treated unordered and all characters were, by default, given equal weight. The matrix was run under the ie*; (implicit enumeration) option of Hennig86 and the branch-and-bound algorithm of PAUP. Both methods guarantee to find all optimal trees (Farris 1988; Swofford 1993).

Using Hennig86, the first six species in the matrix, viz. *cinerella, circumdata, flabellifera, laetabilis, pararecticornis*, and *recticornis*, were selected as the outgroup before the program was run (Hennig86 does not allow the outgroup to be empty; Farris 1988). A methodologically more sound procedure was followed with PAUP, where the complete matrix was used to construct unrooted trees that were afterwards rooted by outgroup rooting (see Nixon & Carpenter 1993 for a recent discussion on the proper use of outgroups). Outgroup rooting of the unrooted trees under PAUP was done in the default fashion, i.e., with the outgroup taxa forming a basal polytomy with the ingroup (Swofford 1993). In this case, the first six species of the data matrix were a posteriori assigned to the outgroup.

Both methods resulted in two equally most parsimonious trees with length 63, consistency index 80 (Hennig86) or 0.810 (PAUP), and retention index 92 (Hennig86) or 0.922 (PAUP). The preferred resulting cladogram is given in fig. 3 and differs from the other equally parsimonious solution by the position of *parallela*. Whereas *parallela* is the sister species of the clade *subfalcata* to *selenaria* in fig. 3, it is the sister species of the clade *bullata* to *selenaria* in the alternative solution. The reasons for preferring the cladogram of fig. 3 will be given below. The results of the phyloge-

Table 2. Character state matrix for *Tipula* (*Lunatipula*) *cinerella, circumdata, flabellifera, laetabilis, pararecticornis, recticornis*, and the species of the T. (L.) *bullata* and *falcata* species groups. ?: unknown or not interpretable; –: inapplicable.

Character				1 0		2 0			3 0		3 6
cinerella	00–10	0---0	11000	00000	00000	00001	00000	0
circumdata	00–10	0---0	11000	00000	00000	00001	00000	0
flabellifera	1100–	101–0	00000	00000	00000	0000?	?????	?
laetabilis	0?–0–	0---0	00000	00000	02000	00000	00000	0
pararecticornis	0100–	0---0	11000	00000	00000	00004	00000	0
recticornis	01010	0---0	11000	00000	00000	0000?	?????	?
bezzii	01011	11–10	00000	01101	10000	00012	01100	0
buchholzi	01011	11–10	00000	01101	10000	00012	01100	0
bullata	01011	11–00	00000	01001	10000	00000	00100	0
cirrata	11010	100–0	00110	03000	01003	10000	10000	2
eyndhoveni	11010	11–00	02011	01000	01003	10003	10000	2
falcata	01110	100–0	00110	01000	01110	00104	10001	1
handschini	11012	101–0	00000	12000	01002	1102?	?????	?
longidens	01110	100–0	00100	01000	01110	00104	10001	0
magnicauda	01110	100–0	00110	01000	01110	00104	10001	1
onusta	01011	11–01	00000	01011	10001	00012	01110	0
parallela	00–10	100–0	00000	00000	01000	00000	00000	0
selenaria	11010	11–00	02011	01000	01003	1000?	?????	?
selenitica	11010	100–0	02000	21000	01003	10200	10200	2
subfalcata	01110	100–0	00100	01000	01110	00004	10001	0
subonusta	01011	11–01	00000	01011	10001	00012	01110	0
subselenitica	11010	100–0	02011	01000	01003	10003	10000	2
trifasciculata	11010	0---0	00100	03000	01003	10000	10000	2
zangherii	11012	101–0	00000	12000	01002	11020	10000	0
zarcoi	11010	0---0	02000	21000	01003	10200	10200	2

netic analysis will be discussed with reference to fig. 3.

A trichotomy uniting *flabellifera*, the clade *laetabilis* to *circumdata*, and the clade *bullata* to *selenaria*, is found at the base of fig. 3. The clade *laetabilis* to *circumdata* is supported by the absence of a posteromedial projection on the aedeagal guide only (character 6). This character state occurs also in *trifasciculata* and *zarcoi*. Future study of the phylogeny of *Lunatipula* must settle the question whether this character stare actually represents an apomorphy at this level of analysis. The examined species of the *recticornis* and *livida* groups (*pararecticornis* and *recticornis*, and *cinerella* and *circumdata*, respectively) together form a monophyletic group supported by the presence of the two-lobed and compressed gonapophyses (character 11) and the shape of the fragmentum (character 12). Both species of the *recticornis* group, however, do not constitute a monophyletic unit. Considering the fact that Savchenko & Theischinger (1978) in their revision of the *recticornis* group did not distinguish any character state that can be considered a synapomorphy for all species of the group, the monophyly of the *recticornis* group seems to be questionable. Both *cinerella* and *circumdata* are united on account of the absence of the dorsal posterolateral extensions of the aedeagal guide (character 2) and the presence of the emarginate apex of the hypogynial valve (character 30). The latter character state is found in all species of the *livida* group.

Fig. 3 depicts the *bullata* and *falcata* groups as two monophyletic units. The *bullata* group is substantiated by four synapomorphies and one homoplasy, the *falcata* group by one synapomorphy. The *bullata* group as distinguished here is identical to the original concept of this group as recognized by Mannheims & Theowald (1959). Within the *bullata* group, *bullata* appears to be the sister species of the remaining four species, which in their turn can be separated inro two species pairs. Mannheims & Theowald appreciated the close relationship of *bezzii* and *buchholzi* on the one hand and, as was expressed by the name giving, that of *onusta* and *subonusta* on the other. As can be inferred from the descriptions of the species given by Mannheims and Theowald, the postulated relationship of *bezzii* and *buchholzi* was primarily inspired by the form of the elongate and single pointed posterior part of the inner gonostylus, that of *onusta* and *subonusta* by the shape of the posterior margin of male tergite 9-10 and the extension of the setal area on male sternite 8. Although these character states are not employed in the present paper, rhe results as regards the hypothesized phylogenetic relationships of the species are the same.

The clade *parallela* to *selenaria* represents the *falcata* group in the sense of the present paper. Mostly because of the structure of the aedeagal guide,

Theischinger (1977) tentatively assigned *parallela* to the *falcata* group with the annotation that the posterior part of the inner gonostylus and posterior margin of tergite 9-10 isolate *parallela* so much that no other species can be regarded as truly closely related. This opinion is reflected in the phylogenetic position of *parallela* in the cladogram adopted here. In the alternative equally parsimonious solution of the phylogenetic analysis, *parallela* is the sister species of the *bullata* and *falcata* groups combined. In the latter case, the presence of a moderately developed posterior part of the inner gonostylus in *parallela* (character 17) is considered primitive and the presence of three setal brushes on the intersegmental membrane of sternites 8 and 9 (character 22) is treated as a homoplasy. Instead of this, I prefer to interpret the presence of a moderately developed posterior part of the inner gonostylus in *parallela* as the result of reduction, as, under reference to fig. 3, must be postulated also to account for the small posterior part in *cirrata* and *trifasciculata*. In the preferred alternative, the three setal brushes on the intersegmental membrane indicate the phylogenetic affinity of *parallela* with the other members of the *falcata* group.

The remainder of species of the *falcata* group consists of two monophyletic groups, the clades *subfalcata* to *magnicauda* and *handschini* to *selenaria*. The first group was recognized by Mannheims (1967) on account of the presence of the extension on the midventral area of the gonocoxites (character 13) and the structure of the posterior part of the inner gonostylus (character 17). The latter character is employed here at a different level in the analysis. Mannheims (1967) did not unequivocally ventilate his views on the interspecific phylogenetic relationships of *falcata*, *longidens*, *magnicauda*, and *subfalcata*. On account of the shape of the posterior margin of male tergite 9-10 (character 28), the length of the anterior part of the inner gonostylus (character 14), and the length of the posterior extension of female sternite 9 (character 36), the relationships as depicted in fig. 3 are postulated.

The clade *handschini* to *selenaria* contains species that are characterized by the absence of a nasus (character 1) and the presence on the intersegmental membrane of male sternites 8 and 9 of setae with a frizzled tip in the dorsal setal brushes (character 26).

The first lineage within the clade *handschini* to *selenaria* leads to the species pair *handschini* and *zangherii*, a monophyletic group which was already isolated as a subgroup within the *falcata* group by Mannheims (1967). Both species are distinguished here from the remainder of the *falcata* group by six synapomorphies and a single homoplasy concerning the aedeagal guide (characters 5, 8), the inner gonostylus (characters 16, 17), the shape of setae in the setal brushes (character

25), and male tergite 9-10 (characters 27, 29).

The sister group of the pair *handschini* and *zangherii*, the clade *cirrata* to *selenaria*, is substantiated by two synapomorphies, one concerning the presence of strong lateral setae in the ventral setal brush on the intersegmental membrane of male sternites 8 and 9 (character 25), the other pertaining to the compressed posterior extension of female sternite 9 (character 36).

Within the clade *cirrata* to *selenaria*, the first lineage contains *cirrata* and *trifasciculata* which are considered sister species on account of the presence of a small posterior part of the inner gonostylus (character 17). Both species also share the presence of a cone-shaped extension on the midventral area of the gonocoxites (character 13), a feature encountered also in the members of the clade *subfalcata* to *magnicauda* and in the unexamined *jativensis* (see below for the presumed phylogenetic position of this species).

Mannheims (1967) grouped the then known species of the clade *selenitica* to *selenaria*, together with *jativensis*, in a subgroup of the *falcata* group. Mannheims supposed that there are close relationships between *jativensis*, *selenitica*, and *zarcoi* and between *selenaria* and *subselenitica*. The phylogenetic analysis presented here substantiates the supposed relationship of *selenitica* and *zarcoi*, which are combined here on account of the sharply emarginate anterolateral part of the inner gonostylus (character 16), the dorsally concave posterior extensions of male tergite 9-10 (character 28), and the presence of a concavity in the lateral sclerotization of female sternite 8 (character 33). The species *selenaria* and *subselenitica* also appear to be closely related, which can be substantiated by the shape of the anterior apex of the anterior part of the inner gonostylus (character 15), the length of the anterior part of the inner gonostylus (character 14), and possibly by the partly fused dorsal and ventral valves in the female (character 30; the female of *selenaria* is not known). The later described *eyndhoveni* probably is the actual sister species of *selenaria*, as can be inferred from the presence of the elongate membranous extension in between the dorsal and ventral posterolateral extensions of the aedeagal guide (character 7). Theowald (1972) introduced *eyndhoveni* under reference to *selenaria*.

Although no material was examined of *jativensis*, information provided by Mannheims (1967) helps to allocate the probable phylogenetic position of this species, which is known from the male holotype only. According to Mannheims, *jativensis* has no nasus (character 1), it has the fragmentum evenly rounded (character 12), it has a membranous extension on the ventromedial area in between the gonocoxites (character 13), while the setae in the dorsal brush of the intersegmental membrane of sternites 8 and 9 are friz-zled at their tips (character 26). This combination of character states suggests a sister group relationship of *jativensis* and the species pair *cirrata* and *trifasciculata*, thus contradicting Mannheims' view (1967) that *jativensis* is more closely related to species now contained in the clade *selenitica* to *selenaria*.

DISTRIBUTION

This section provides a brief account on the distribution of the species of the *bullata* and *falcata* groups. As noted above, more detailed information on the distribution of these species will be given in a forthcoming paper on the historical biogeography of the western Mediterranean. The sequence of taxa in the summary below follows that of fig. 3.

The *bullata* group is primarily distributed in Italy (fig. 2). The most widespread species of this group is *bullata*, which is known from the secondary mountain-chains in central Europe. It has been found in the eastern Ardennes and neighbouring Eifel, south-eastern France, the Alps and adjacent mountainous areas. It seems to be absent though from the Pyrenees, Apennines and Carpathians. Martinovsky (1987) reported *bullata* for the first time from Slovakia.

The species *bezzii* seems to be restricted to lower areas as it occurs along the coast of southern France and in the valley of the Po in northern Italy. The single known Swiss specimen of *bezzii* was captured at an altitude of 340 meters (Dufour 1986). The species *buchholzi* is endemic to Italy, where it has been recorded from the Apennines in the north to Calabria in the south. About the same range is shown by *onusta*, which is also known from Croatia (Simova-Tosic & Vukovic 1981). The species *subonusta* is endemic to Sicily.

The *falcata* group is more widespread than the *bullata* group (fig. 2). As far as available records show, *parallela* seems to be distributed over the entire Iberian Peninsula. The range of *subfalcata* extends over central and southern Spain and the Rif mountains of northern Morocco. The species *longidens* has a wider range, with the centre of distribution lying in central and northern Spain. It is also known from a few localities in central France, western Switzerland, south-eastern Belgium and eastern Germany. The distribution area of *falcata* ranges from the southern border of Switzerland southward to Calabria and the eastern tip of Sicily. Its sister species *magnicauda* is distributed in the Ardennes in Belgium, the Eifel in Germany, and the Alps. Martinovsky (1987) recorded *magnicauda* for the first time from Bohemia in the present-day Czech Republic and also reported the first find of this species for Poland (Martinovsky in litt.).

The species pair *handschini* and *zangherii* is primarily distributed over Italy, with *handschini* occurring in

the Alps and southern Italy, and *zangherii* in northern and central Italy. A single male of *handschini* has been recorded from south-west Switzerland by Dufour (1986).

The newly described *cirrata* is known from southeast Spain, its sister species *trifasciculata* is distributed in central and southern Spain. The species *selenitica* is known from Portugal, north-west Spain, the Pyrenees, and south-eastern France. Pierre (1924) claimed that *selenitica* also occurred in the environment of Paris, France. The presumed sister species of *selenitica*, *zarcoi*, is endemic to Spain, where it has been recorded from several provinces in the central and southern part of the country. Another endemic Spanish species with about the same range as *zarcoi* is *subselenitica*. The two remaining species of the *falcata* group are endemics to north-west Africa, viz. *eyndhoveni*, which is known from the type locality in northern Algeria only, and *selenaria*, which occurs in the High and Middle Atlas of Morocco. As far as presently known, there are no species of the *bullata* and *falcata* groups recorded from Corsica or Sardinia.

REFERENCES

Alexander, C. P., 1942. See Alexander 1966.
Alexander, C. P., 1946. Records and descriptions of North American crane-flies (Diptera) part VI. Tipuloidea of Arizona, New Mexico and trans-Pecos Texas, I. – The American Midland Naturalist 35: 484-531.
Alexander, C. P., 1947. Undescribed species of crane-flies from the western United States and Canada (Dipt.: Tipulidae). Part VII. – Entomological News 58: 61-67.
Alexander, C. P., 1965. New subgenera and species of crane-flies from California (Diptera: Tipulidae). – Pacific Insects 7: 333-386.
Alexander, C. P., 1966. Family Tipulidae. – In: Crampton,

G. C. et al. (eds.) Guide to the insects of Connecticut. Part VI. The Diptera or true flies of Connecticut. First fascicle. Bulletin of the Connecticut State Geological and Natural History Survey 64: 196-486b. (Reprint of Alexander 1942).
Alexander, C. P., 1967. The crane flies of California. – Bulletin of the California Insect Survey 8: 1-269.
Dufour, C., 1986. Les Tipulidae de Suisse (Diptera, Nematocera). – Documenta Faunistica Helvetiae 2: 1-187, + 1-149.
Edwards, F. W., 1931. Some suggestions on the classification of the genus *Tipula* (Diptera, Tipulidae). – Annals and Magazine of Natural History (10) 8: 73-82.
Farris, J. S., 1988. Hennig86, version 1.5 + reference. – Port Jefferson Station, New York.
Frommer, S. I., 1963. Gross morphological studies of the reproductive system in representative North American crane flies (Diptera: Tipulidae). – Kansas University Science Bulletin 44: 535-626, pls. I-XX.
McAlpine, J. F., 1981. Morphology and terminology - adults. – In: McAlpine, J. F. et al. (eds.) Manual of Nearctic Diptera. Volume 1. Research Branch, Agriculture Canada, Monograph 27: 9-63.
Maddison, W. P., 1993. Missing data and missing characters in phylogenetic analysis. – Systematic Biology 42: 576-581.
Mannheims, B., 1951. Tipulidae. – Fliegen der Palaearktischen Region 15, Lieferung 167: 1-64, pls. I-VII.
Mannheims, B., 1963. Tipulidae. – Fliegen der Palaearktischen Region 15, Lieferung 238: 137-176.
Mannheims, B., 1965a. Tipulidae. – Fliegen der Palaearktischen Region 15, Lieferung 256: 177-212.
Mannheims, B., 1965b. Enumeratio Tipulidarum Fenniae. – Lounais-Hämeen Luonto 20: 1-3.
Mannheims, B., 1966. Tipulidae. – Fliegen der Palaearktischen Region 15, Lieferung 267: 213-256.
Mannheims, B., 1967. Tipulidae. – Fliegen der Palaearktischen Region 15, Lieferung 270: 257-288.
Mannheims, B., 1968. Tipulidae. – Fliegen der Palaearktischen Region 15, Lieferung 275: 289-320.
Mannheims, B. & E. Pechlaner, 1963. Die Tipuliden Nordtirols (Dipt.). – Stuttgarter Beiträge zur Naturkunde 102: 1-29.
Mannheims, B. & B. Theowald, 1959. Die Tipuliden Italiens (Dipt., Tipulidae). – Memorie della Società Entomologica Italiana 38: 15-54.
Martinovsky, J., 1987. Tipulidae. – Acta Entomologica Musei Nationalis Pragae 18: 11-14.
Nixon, K. C. & J. M. Carpenter, 1993. On outgroups. – Cladistics 9: 413-426.
Oosterbroek, P. & B. Theowald, 1992. Family Tipulidae. – Catalogue of Palaearctic Diptera 1: 56-178.
Pierre, C., 1924. Diptères: Tipulidae. – Fauna de France 8: 1-159.
Platnick, N. I., C. E. Griswold & J. A. Coddington, 1991. On missing entries in cladistic analysis. – Cladistics 7: 337-343.
Rees, B. E. & G. F. Ferris, 1939. The morphology of *Tipula reesi* Alexander (Diptera: Tipulidae). – Microentomology 4: 143-178.
Riedel, M. P., 1913. Die paläarktischen Arten der Dipteren- (Nematocera polyneura-) Gattung *Tipula* L. (Dipt.). – Abhandlungen des Vereins für Naturwissenschaftliche Erforschung der Niederrheins- (Bezirksgruppe des deutschen Lehrervereins für Naturkunde.) I. Band 1913: 1-

122, pls. I-III.

Savchenko, E. N., 1964. Crane flies (Fam. Tipulidae), sub-fam. Tipulinae: genus *Tipula* L. (part 2). – Fauna SSSR (N.S. 89) Two-winged insects II (4): 1-502. (In Russian).

Savchenko, E. N. (as Savtshenko) & G. Theischinger, 1978. Die Arten der *Tipula* (*Lunatipula*) *recticornis*-Gruppe (Diptera, Tipulidae). – Bulletin Zoologisch Museum, Universiteit van Amsterdam 6: 117-128.

Simova-Tosic, D. & M. Vukovic, 1981. The results of crane flies (Diptera, Tipulidae) studies in Yugoslavia. – Acta Entomologica Jugoslavica 17: 113-119.

Simova-Tosic, D. & M. Vukovic, 1983. The significance of the male genitalia for identification of the crane flies species (Tipulidae, Diptera). – Acta Entomologica Jugoslavica 19: 27-32. (In Serbo-Croatian, English summary).

Swofford, D. L., 1993. PAUP, Phylogenetic Analysis Using Parsimony, version 3.1. – Illinois Natural History Survey, Champaign, Illinois.

Tangelder, I. R. M., 1985. Phylogeny of the *Nephrotoma dorsalis* species-group (Diptera, Tipulidae), mainly based on genital characters. –Beaufortia 35: 135-174.

Theischinger, G., 1977. Neue Taxa von *Lunatipula* Edwards aus der mediterranen Subregion der Paläearktis (Diptera, Tipulidae, *Tipula* Linnaeus). – Beaufortia 26: 1-38.

Theischinger, G., 1979a. Neue Taxa von *Lunatipula* Edwards aus der mediterranen Subregion der Palaearktis (Diptera, Tipulidae, *Tipula* Linnaeus). I. Fortsetzung. – Beaufortia 28: 121-150.

Theischinger, G., 1979b. Über *Lunatipula* aus Afghanistan (Diptera, Tipulidae, *Tipula* Linnaeus). – Bulletin Zoologisch Museum, Universiteit van Amsterdam 6: 145-150.

Theischinger, G., 1979c. Neue Taxa von *Lunatipula* Edwards aus der mediterranen Subregion der Palaearktis (Diptera, Tipulidae, *Tipula* Linnaeus). II. Fortsetzung. – Beaufortia 29: 275-308.

Theischinger, G., 1980. Neue Taxa von *Lunatipula* Edwards aus der mediterranen Subregion der Palaearktis (Diptera, Tipulidae, *Tipula* Linnaeus). III. Fortsetzung. – Beaufortia 30: 17-29.

Theischinger, G., 1982. Neue Taxa von *Lunatipula* Edwards aus der mediterranen Subregion der Palaearktis (Diptera, Tipulidae, *Tipula* Linnaeus). IV. Fortsetzung. – Beaufortia 32: 79-96.

Theischinger, G., 1987. Neue Taxa von *Lunatipula* Edwards aus der mediterranen Subregion der Palaearktis (Diptera, Tipulidae, *Tipula* Linnaeus). V. Fortsetzung. – Beaufortia 37: 99-120.

Theowald, B., 1957. Die Entwicklungsstadien der Tipuliden (Diptera, Nematocera), insbesondere der west-palaearktischen Arten. – Tijdschrift voor Entomologie 100: 195-308.

Theowald, B., 1967. Familie Tipulidae. (Diptera, Nematocera). Larven und Puppen. – Bestimmungsbücher zur Bodenfauna Europas 7: 1-100.

Theowald, B., 1972. Die Tipuliden Algeriens (Diptera, Tipulidae). – Entomologische Berichten 32: 3-5.

Theowald, B. & P. Oosterbroek, 1990. Zur Zoogeographie der westpaläarktischen Tipuliden. IX. Die Tipuliden des Vorderen Orients. – Tijdschrift voor Entomologie 133: 85-95.

Tjeder, B., 1958. A synopsis of the Swedish Tipulidae, I. Subfam. Limoniinae: tribe Limoniini. – Opuscula Entomologica 23: 133-169.
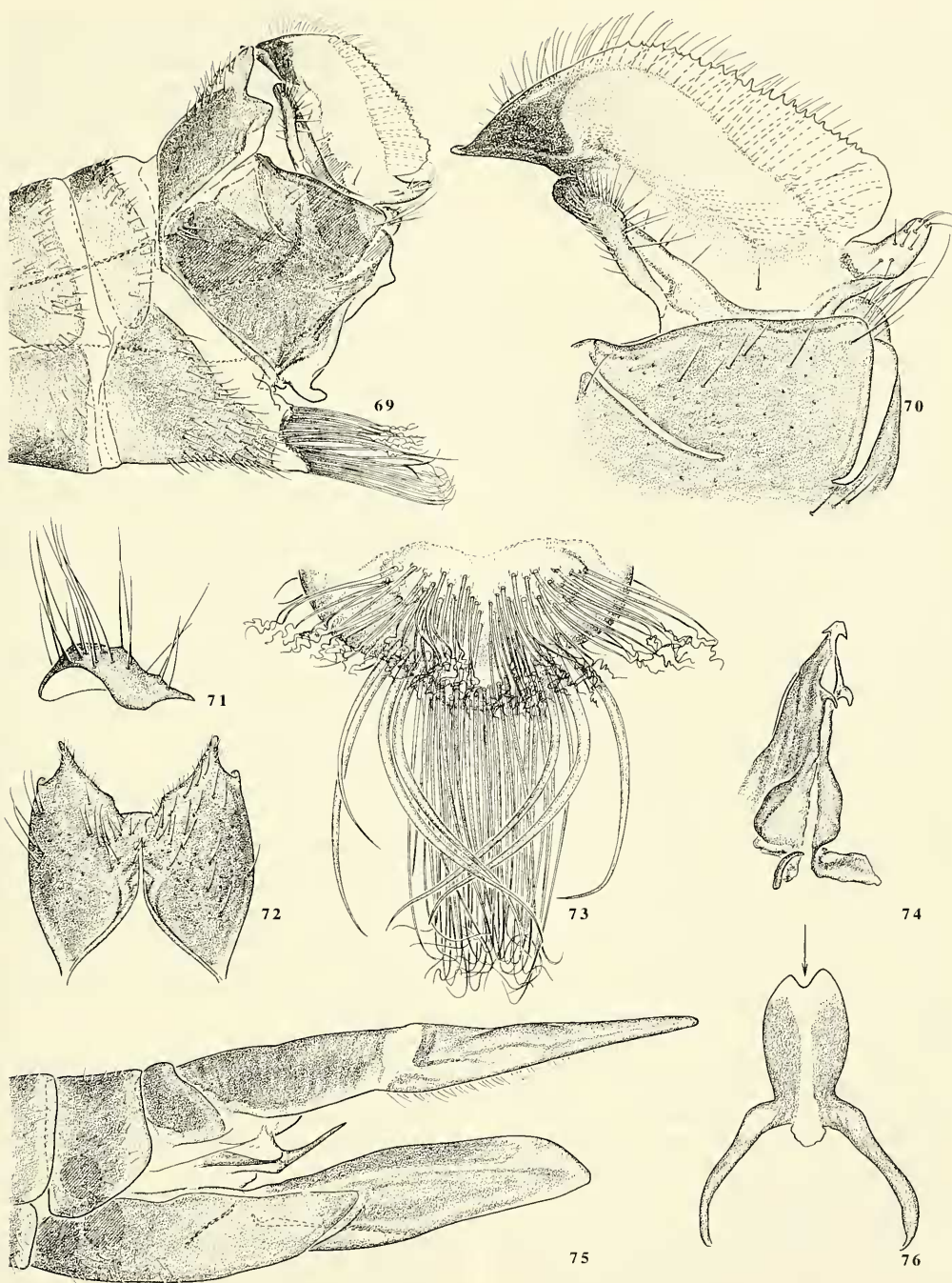
Figs. 69-76, *Tipula* (*Lunatipula*) *cirrata* sp.n.; 69, male terminalia, lateral view; 70, left inner and outer gonostyli, lateral view; 71, left fragmentum, dorsal view; 72, tergite 9-10, dorsal view; 73, setal brushes on intersegmental membrane sternites 8 and 9, posterior view; 74, aedeagal guide and appendages, posterolateral view; 75, female terminalia, lateral view; 76, female sternite 9, ventral view.

Appendix A

Tipula (Lunatipula) cirrata sp.n.
(figs. 69-76)

Type material. – Holotype ♂: Spain, Jaén, Sierra de Cazorla, Rio Guadalquivir, 900 m, 22.IV.1994, P. Oosterbroek & C. Hartveld (ZMAN). – Paratypes: 2♂, same data as holotype; 3♂, 1♀, Spain, Jaén, Sierra de Cazorla, Rio Aguamula, 700 m, 23.IV.1994, P. Oosterbroek & C. Hartveld (ZMAN).

Description

Body length 15.5-17 mm (♂), 20 mm (♀); wing length 15.5-18 mm (♂), 15.5 mm (♀); antennal length 4.2-4.8 mm (♂), 2.8 mm (♀).

Colour. – Ground colour light brown, head and thorax extensively brownish-grey pruinose. Anterior part of rostrum and vertex dorsally with dark brown median vitta. Antenna with scape and pedicel light brown, dorsolaterally brownish-grey pruinose, first flagellomere basally light brown becoming darker towards tip, remainder of flagellum dark brown. Palpus brown, dorsally and apically darker. Pronotum with dark brown medial vitta. Prescutum with two pairs of broad dark brown stripes, medial pair separated by broad lighter stripe. Scutellum and metatergite with dark brown medial vitta indicated. Wing veins dark brown, pterostigma dark brown, distinct. Membrane darkish coloured, except for yellowish subcostal cell and anterior margin of cubital cell, pale area in front of pterostigma reaching base of cell m3. Haltere with light brown stem, knob largely dark brown. Coxae greyish pruinose, pruinosity less dense on posterior pairs of legs. Trochanters and base of femora light brown, femora becoming dark brown towards apex. Tibiae brown, becoming darker towards tips, remainder of legs dark brown. Abdomen light brown, with broad dark brown continuous medial stripe on tergites 1 to 7 and less distinct dark brown sublateral stripe on tergites 2 to 6, tergite 8 light brown, accompanying sternite and following segments of abdomen darker brown.

Head. – Rostrum about as long as remainder of head, nasus absent. Eyes dorsally and ventrally separated by about 2.5 times diameter of scape. Antenna with five verticils in whorl at base of flagellomeres, the two medial ones short, the dorsally and laterally placed ones longer, longest verticils slightly longer than length of flagellomere.

Thorax. – Wing fully developed in both sexes, squama with about ten distinct macrotrichia. Tarsal claws with medial tooth in male, toothless in female.

Male terminalia (figs. 69-74). – Sternite 8 at posterior margin in intersegmental membrane with single ventral and pair of dorsal setal brushes. Setae of brushes about as long as greatest length of sternite 8, those of dorsal brushes curled at tip. Medial setae of ventral brush wavy at tip, ventral brush laterally with two setae about twice the diameter of the remainder of setae (fig. 73). Tergite 9-10 and gonocoxites separated by membranous zone (fig. 69). Tergite 9-10 (fig. 72) broad and short, with narrow medial membranous area. Anterior margin of tergite 9-10 V-shaped, posterior margin widely U-shaped, posterolateral extensions narrow in dorsal view. Posterodorsal part of gonocoxite incompletely separated from the remainder of gonocoxite by sutures, this part of gonocoxite not produced (fig. 70). Fragmentum a broad sclerotized low lobe set with scattered long golden yellow setae (fig. 71). Midventral area in between gonocoxites membranous, lateral margins diverging posteriorly, anteriorly carrying membranous conical extension (fig. 69). Sp2 small, squarish, moderately sclerotized. Foramen of gonostyli medially very weakly sclerotized to membranous. Sp1 small, V-shaped, separate from sp2. Outer gonostylus (fig. 70) short and slender, slightly broader at apex. Inner gonostylus (fig. 70) with large anterior part provided with serrate dorsal crest, posterior part short, lateral carrying a few setae. Inner gonostylus medially provided with sensory area at base of posterior part. Proctiger entirely membranous. Aedeagal guide (fig. 74) a compact sclerotized structure, at tip with dorsal and ventral pair of posterolateral extensions. Sperm pump with anterior and posterior apodemes short, compressor apodeme dorsally deeply emarginate, lumen well-developed, body strongly convex. Aedeagus long, slender, tubular throughout, anteriorly reaching abdominal segment 1.

Female terminalia (figs. 75, 76). – Cercus in lateral view with almost straight margins, tapering to tip. Sternite 8 dorsolaterally near base of hypogynial valve ending in acute angle. Hypogynial valve strong, pointed at lower posterior corner (fig. 75). Sternite 9 with broad and dorsoventrally compressed posterior extension (fig. 76). Three spermathecae, oblong oval, spermathecal duct rotated at base.

Etymology. – The name cirrata, an adjective in the nominative singular, refers to the presence of frizzled setae in the brushes on the intersegmental membrane of male sternites 8 and 9. Cirratus (Latin) means with curly hairs.

Remarks. – As the above given phylogenetic analysis shows, cirrata is closely related to trifasciculata. Differences are found in the shape of the inner gonostylus, which in trifasciculata has a shorter and dorsally rounded anterior part (fig. 31) compared to that of cirrata (fig. 70), in the structure of the posterior margin of male tergite 9-10, which in trifasciculata has shorter posterior extensions, in the shape of

the fragmentum, which is higher in *trifasciculata* (fig. 22; cf. fig. 71), in the length of the female cerci, which are shorter in *trifasciculata*, and in the tip of the posterior extension of female sternite 9, which is acute in *trifasciculata* and emarginate in *cirrata* (fig. 76).

APPENDIX B

Autapomorphies of the species of the *Tipula* (*Lunatipula*) *bullata* and *falcata* groups

267